Mode of Feeding and Diet, and Synthesis of Studies on Marine Pelecypods from Tomales Bay, California

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INTRODUCTION

THE PRESENT INVESTIGATION has a threefold purpose: 1) To describe the mode of feeding and diet of bivalves previously unreported; 2) To provide further evidence to interpret pelecypod-sediment associations described in an earlier study; 3) To synthesize field and laboratory work heretofore treated separately.

In a series of papers on marine pelecypods from Tomales Bay, California, I have been primarily concerned with the ecology of bivalves in relation to sediment and the interpretation of these relationships. More specifically, MAURER (1967) reported on the relationship between distribution, abundance, and size of *Tellina buttoni* DALL, 1900, *T. salmonea* (CARPENTER, 1864), *Mysella tumida* (CARPENTER, 1864), *Transennella tantilla* (GOULD, 1852), and *Lyonsia californica* CONRAD, 1837, to sediment type. In addition, MAURER (1967 a, 1967 b) described filtering and burial experiments respectively to explain the response of mollusks to sediment. One observation which emerged from these experiments was that, at least for a few of the pelecypods, the sediment might represent an important food source, or that their mode of feeding may be dependent on the type of substrate in which they live. If this is true some of the pelecypod-sediment associations recognized by the author might be accounted for.

STEPHEN (1928, 1929, 1930, 1932), HOLME (1949, 1961), YONGE (1949), SANDERS (1958, 1962), and POHLO (1966) have contributed information on feeding habits of tellinids. At present there are very few data on feeding of *Tellina buttoni* and *Tellina salmonea*, or, for that matter, on any of the other species treated in the study. The following discussion is restricted mainly to the tellinids and *Transennella tantilla* with some brief comments on *Mysella tumida* and *Lyonsia californica*.

OBSERVATIONS

Siphons of *Tellina buttoni* are separate, long and flexible. The exhalant siphon is slender and tapers towards the aperture, while the inhalant siphon, which terminates abruptly, is more muscular than the exhalant siphon. On a conservative estimate, *T. buttoni* may extend its siphons four or five times the shell length which varied from 0.19 to 1.85 cm in length.

In an aquarium when *Tellina buttoni* burrowed into the substrate, it would gently test the sediment with its inhalant siphon and begin to inhale the substrate like an elephant's trunk. This feeding behavior of *T. buttoni* compares favorably with that of British tellinids described by YONGE (1949). *Tellina buttoni* has also been observed to probe the substrate with its inhalant siphon. Suction from its siphon disturbs sediment and causes fine matter to be raised into suspension. The mollusk then inhales the suspended particulate material.

During filtering experiments it was noticed that test animals would occasionally reach up with their inhalant siphons and take carmine particles out of suspension (MAURER, 1967 a). Nevertheless, the inhalant siphon was usually occupied with the bottom deposits or material raised by its movements into suspension just above the bottom.

During burial experiments *Tellina buttoni* would rarely, if ever, form any holes in the overlying clay (MAURER, 1967 b). And depending on the thickness of clay it would almost never extend its siphons above the clay-water interface. Following the burial experiments siphons of dead *T. buttoni* were frequently packed with clay and test animals that survived invariably contained some clay. For *T. buttoni* there was increased ingestion of clay with increased amounts of clay used in the experiments.

Concerning the diet of *Tellina buttoni* some preliminary observations can be offered. Diatoms were extremely abundant in outdoor aquaria where the clams were maintained. Upon dissection *T. buttoni* was found to be full of needle-like species of *Navicula*. This diatom lay obliquely in ctenidial chambers of the bivalves blocking water circulation. Other diatoms, *Coscinodiscus* and *Bidulphia*, were observed to be scattered throughout the alimentary tract and stomach. It is unknown whether *T. buttoni* ingests such large quantities of diatoms in nature. An unsuccessful attempt was made to identify stomach contents of freshly preserved material aboard ship. However, material found in feces of bivalves just after collection consisted of quartz, biotite, quartz diorite, schist, and the foraminifer *Elphidium*. An empty ostracod carapace was found in the area of the digestive gland of one of these mollusks. Several days after these pelecypods had been placed in aquaria with glass beads as substrate, they were examined and found to contain glass beads in the alimentary tract.

Several citations to feeding of tellinids in nature can be alluded to. For example, STEPHEN (1928) noticed that during the spring diatoms appeared almost exclusively in the gut of several species of *Tellina*. YONGE (1949) reported that a species of *Macoma* fed on deposits rich in diatoms. SANDERS *et al* (1962) listed a species of *Tellina* as containing sand, diatoms, and detritus in its stomach.

Both *Tellina salmonea* and *T. buttoni* have well developed longitudinal and transverse muscles in their siphons and a cruciform muscle that is characteristic of members of the Tellinacea (YONGE, 1949). The muscle is a sheath of fine, tough fibers attached ventrally to the base of the siphons and contributes to the flexibility and siphonal activity of forms with long siphons. Moreover, the siphons of *Tellina salmonea* are translucent, and as seen in *T. buttoni*, its siphons may extend 4 or 5 times the shell length which varied from 0.20 to 1.87 cm in length.

When *Tellina salmonea* was placed in aquaria without any substrate it would almost immediately raise its siphons up into the water. When sediment was present, its inhalant siphon would settle upon and probe the substrate, alternating continuously from water to substrate. For the main part siphons of *T. salmonea* were characteristically in the water as it would often function as a suspension feeder. Duality of feeding habit exhibited by this tellinid is even more marked than that of *T. buttoni*, and *T. salmonea* showed a preference for suspension feeding. HOLME (1961) has suggested a dual feeding habit for a British tellinid as he described the disposition of its siphons while feeding. He concluded that it may be able to feed as a suspension feeder and is probably not restricted to a deposit feeding habit. POHLO (1966), who worked on *Tagelus californianus* (CONRAD, 1837), another tellinid which occurs in Tomales Bay, stated that it was not an active deposit feeder, but that it fed on suspended material. These references and my observations indicate that tellinids are not as restricted to a deposit feeding habit as was previously thought.

In filtering experiments *Tellina salmonea* had the lowest filtering rate (MAURER, 1967a). Yet it was commonly observed to inhale suspended carmine particles. Depending on the thickness of clay in the burial experiments *T. salmonea* would form holes in the heavy, viscous clay (MAURER, 1967b). This behavior was never observed in *T. buttoni*. Siphons of *T. salmonea* were rarely packed with clay, whereas siphons of the other tellinid were generally filled. ARMSTRONG (1965) described the difficulty encountered by clams covered by sand. Unless bivalves could extend their siphons through the new cover to the surface or maintain a sand free passage, they would perish. This might explain in part the high mortality of *T. buttoni* in the burial experiments.

Concerning the diet of *Tellina salmonea* it was observed to inhale copepods and the diatom *Coscinodiscus* which was extracted from the gills of this tellinid. These diatoms were also found in the stomach, and chains of diatoms were noticed in the digestive tract as well. Although *T. salmonea* was maintained in aquaria under conditions similar to *T. buttoni*, at no time was *T. salmonea* observed to be filled with diatoms or contain as much detrital material as *T. buttoni*.

Only a few general comments on the mode of feeding and diet of *Transennella tantilla*, *Mysella tumida*, and *Lyonsia californica* can be offered. Siphons of *Tr. tantilla* are short and free distally, but fuse proximally. Siphons contain frills or small tentacles around the apertures and this tentacular arrangement seems to be characteristic of many suspension feeders. In filtering experiments *Tr. tantilla* had a relatively high filtering rate and was seen to inhale suspended carmine and India ink particles. In burial experiments it suffered the least amount of mortalities and survived the rigors of the viscous clay. The fact that *Tr. tantilla* occurs intertidally to subtidally might be accounted for by its ability to remain shut for long periods of time, and thereby circumvent the deleterious conditions imposed by the overlying clay. The diatoms *Navicula*, *Bidulphia*, and *Coscinodiscus*, which were dissected from the other test species, were also found in *Tr. tantilla*. In addition, *Nitzschia* and *Melosira* were discovered within its gill system. These examinations were made on specimens that had lived in the outdoor aquaria for several weeks. Examination of specimens which had remained in the aquaria a couple of days showed some glass beads, quartz, and shell fragments in their feces.

Mysella tumida was observed to feed on copepods and diatoms and the latter were dissected from the stomach. Upon dissection of *Lyonsia californica* no debris was found in its stomach. Other than this no observations were recorded on diet or mode of feeding of *L. californica.* Kellogg (1915) briefly described and figured *L. saxicola* (Baird, 1863) and he stated that its ciliary mechanism was very similar to that of *L. californica.* On this tenuous basis it is provisionally suggested that *L. californica* is a suspension feeder.

DISCUSSION

Results of field studies by Swan (1952), Pratt (1953), Pratt & Campbell (1956), and Kristensen (1957) indicated that size of *Mya arenaria* Linnaeus, 1758, *Venus mercenaria* (Linnaeus, 1758) and *Cardium edule* Linnaeus, 1758 may be strongly influenced by turbidity, rate of sedimentation, and nature of the substrate. Moreover, Maurer (1967) arrived at a similar conclusion concerning the distribution and abundance of *Lyonsia californica, Tellina buttoni, Tellina salmonea,* and *Mysella tumida* in Tomales Bay, California. Further it was revealed that the average size of the latter 3 species was statistically associated with sediment particle size. Laboratory studies referred to in Allen's (1963) review and especially the work of Loosanoff and co-workers showed the deleterious effects of increased sedimentation (organic and inorganic particles) on respiratory and feeding activities of *Mytilus edulis* Linnaeus, 1758, *Crassostrea virginica,* and *Venus mercenaria.* About the response of different ctenidial types to filtering experiments it might be pointed out that *Mytilus edulis* is a filibranch, *Crassostrea virginica* is a pseudolamellibranch, and *Venus mercenaria* is a eulamellibranch; however, all feed as suspension feeders. Evidence on harmful effects of increased sedimentation to bivalves was provided by Maurer (1967a, b). Results of these experiments on mollusks from Tomales Bay agree generally with those cited from the literature.

Since the recognition of the pelecypod-sediment associations, one of the main objects of the investigation has been to obtain information concerning response of mollusks to sediment, in terms of food, protection, larval sites, and turbidity. From experiments and observations the author considers, at least for a few of the pelecypods, that sediment as a food source may dictate mode of feeding or that certain conditions of turbidity are related to the deposition of particular sediment types.

On the effect of turbidity on distribution, abundance, and size of clams it has been asserted that an increase or inhibition of growth might be related to sediment. Pelecypods that live in turbid environments waste energy in clearing palps and gills from excessive particulate matter, produce greater amounts of pseudofeces, and consequently spend less time feeding. On the other hand, in a relatively clean environment the mollusks obtain maximal nutritional benefit of feeding time. Turbid conditions inhibit growth; clean conditions foster it. Pratt & Campbell (1956) clearly stated this proposition in their study of *Venus mercenaria* and Loosanoff (1962) voiced a similar opinion. The present author considers this effect of sediment or sedimentation to be an important factor influencing the pelecypod-sediment associations with which he was concerned.

SYNTHESIS of FIELD and LABORATORY STUDIES

For *Tellina buttoni* statistical analyses indicated that average size was positively associated with sediment size (Maurer, 1967). Laboratory work suggested some interesting features that might account for the association on the basis of turbidity tolerance and mode of feeding. Filtering ability of *T. buttoni* was generally high and it has been observed to inhale suspended material. Yet even with small concentrations used in the filtering experiments, *T. buttoni* commonly ingested more ink, carmine, and clay particles than *Tellina salmonea* and *Transennella tantilla.* In burial experiments *Tellina buttoni* again ingested large amounts of clay that it was generally unable to handle and these amounts were almost always greater than in the other test animals. Furthermore its production of pseudofeces was usually greater in heavier loads of clay. The relative amount of pseudofeces formed agreed substantially with that of other bivalves exposed to excessive amounts of material described by Loosanoff (1962). These mollusks were suspension feeders and had different ctenidial structures than *T. buttoni.* The preference of *T. buttoni* for silty-sand in light of laboratory work indicates that this species functions chiefly as a deposit feeder. The same evidence also indicates that there is a critical sediment size which inhibits growth. Sediment, which contains more than 30% silt and clay, is probably deposited in a turbid environment and is too densely packed to allow easy use of siphons to filter, feed, and digest efficiently.

For *Tellina salmonea* statistical analyses showed that average size was positively associated with sediment size (Maurer, 1967). Laboratory work revealed some interesting adaptations. As with *T. buttoni,* the association may be explained on similar grounds, that is, food and tolerance to turbidity. With *T. salmonea* the siphons were generally extended above the substrate, but were occasionally seen to inhale bottom deposits. Contrary to this in the filtering experiments it had the lowest filtering rate and in the burial experiments *T. salmonea* was rarely full of clay. Distribution of this tellinid in substrates that range in particle size from silt through pebbles, particularly in the coarse sediment, suggests a suspension feeding habit. It was not clear whether *T. salmonea* was more sensitive to turbid conditions or had more difficulty inhaling large amounts of clay and silt than *T. buttoni*. On the basis of its more limited distribution in coarse sediment it is suggested that *T. salmonea* is more sensitive to turbid conditions than *T. buttoni*. When *T. salmonea* occurred in sediment with as much as 30% silt and clay, its size was limited and it was smaller than individuals which lived in sediment with little or no particulate material. In view of laboratory studies the preference of *T. salmonea* for detritus-free, medium sand to shell-sand indicates that this species functions as a suspension feeder in clean, coarse sediment and as a deposit feeder in fine substrates. This result tends to confirm suspicions raised by MAURER (1967 a) on possible dual feeding habit of *T. salmonea* and *T. buttoni*.

For *Mysella tumida* statistical analyses showed that average size was negatively associated with sediment size. From its distribution in sediment types comparable to the distribution of *Tellina buttoni*, and its single performance in the filtering experiments, it is tentatively concluded that *M. tumida* can filter fine material better than the tellinids. Studies by BALLENTINE & MORTON (1956) showed that a closely related genus was a suspension feeder which could feed selectively on diatoms. It appears that the distribution, abundance, and size of *M. tumida* is influenced by sediment size. However, its negative association with sediment size indicates that conditions of turbidity or sediment as a source of food do not have the same effect on *M. tumida* as they do on the tellinids.

Average size of *Transennella tantilla* did not show a significant association with sediment size (MAURER, 1967). Its ubiquitous distribution in the bay seemed to illustrate its independence from characteristic sediment types. Laboratory work did not disclose any dual feeding habit as was noticed in the tellinids. Relatively high filtering efficiency, low mortality rate and absence of clogging in burial experiments, tentacular frill work on siphons define *Tr. tantilla* as a suspension feeder. It was concluded that sediment does not exert a controlling influence on distribution, abundance, and size of *Tr. tantilla* as it does on the tellinids and *Mysella tumida*.

Although *Lyonsia californica* had no significant pelecypod size - sediment size associations, its maximal distribution and abundance were found to be in mud with 85% to 100% silt and clay. It appears that *L. californica* is adapted to extremely turbid conditions and heavy sedimentation encountered in the southern portion of the bay. The nature of these adaptations has not been examined, but work on the functional morphology of its feeding apparatus would probably explain its rather restricted occurrence in very fine sediment.

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